Behavioral Changes in the Army Ant *Neivamyrmex nigrescens* during the Nomadic and Statary Phases

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Abstract: The responses of workers of the army ant *Neivamyrmex nigrescens* to illumination and to the presence of conspecifics were compared during the nomadic and statary phases. During the statary phase the ants were more photonegative and exhibited a stronger tendency to cluster together than during the nomadic phase. It is hypothesized that these differences in the ants' orientation are caused by corresponding changes in the level of the colony excitation during the two phases of each behavioral cycle.

Introduction

Colonies of the army ant *Neivamyrmex nigrescens* Cresson exhibit cycles of alternating nomadic and statary phases. The nomadic phase, which lasts for 17–20 days, is one of high colony activity, in which large nightly raids typically end in emigrations to new nesting sites. During this phase raiding begins early in the evening, and a considerable portion of the adult worker population participates (Schneirla, 1958, 1963, 1971). As the raid progresses, one or more dendritic systems of interconnecting trails arise through the repeated division of small terminal foraging groups of ants. The outward movement of the ants from the nest may remain at a peak for up to several hours, because the ants' high level of excitement persists both at the raiding fronts and on the basal column extending to the nest (Schneirla, 1971).

The nomadic phase is followed by a statary interval of 17–20 days, characterized primarily by the absence of emigrations. Raiding is also less vigorous, with fewer individuals participating. Statary raids usually consist of a single, long basal column which ends in a small and localized terminal branching system. The outward surge of ants at the start of raiding usually peaks after only a few minutes. As a result, the basal column remains relatively thin throughout the night.

The cycles of activity in *N. nigrescens* are regulated by stimulative relationships between the colony's developing brood and the adult worker population. During the nomadic phase, the adult workers are aroused to a high level of excitement by stimuli originating from the newly eclosed callow workers and from the maturing larval brood. When the larvae pupate the excitatory stimuli decrease and the colony lapses into the "quieter" statary phase (Schneirla, 1957, 1971).

According to Schneirla's theory, workers of *N. nigrescens* are aroused to very different levels of excitement during the two phases of each behavioral cycle. It is possible that many aspects of each ant's physiological and behavioral condition are affected by changes in the stimulative relationships among all individuals in the colony throughout each cycle. These may include changes in the ants' responsiveness to a variety of physical and biotic stimuli. Accordingly, I conducted a series of tests designed to compare the responses of adult workers of *N. nigrescens* to photic stimulation and to stimuli arising from other workers during the nomadic and statary phases. The objective was to correlate phase-specific differences in the behavior of the ants in the laboratory tests with our observations of colony behavior in the field.

METHODS

Tests were conducted at the Southwestern Research Station of The American Museum of Natural History, in Portal, Arizona. The apparatus used to measure the ants' responses to light consisted of a cylindrical arena (30.0 cm diam × 2.5 cm high) that was divided into five equal areas by a combination of opaque rectangular partitions and a central cylindrical cartridge (Fig. 1). The arena was illuminated from above by a 22-watt fluorescent light ring, and the light was diffused through a disc of neutral ground glass. Two neutral density filters were placed on the lid of the arena to reduce the intensity of light in 2 opposite chambers of the arena (Fig. 1). The intensity of illumination in the central cartridge and in 2 opposite chambers of the arena was 16,000 lux; the intensity of illumination in the remaining 2 chambers was reduced to 160 lux.

The central cartridge had 4 equidistant slit-like openings at the bottom, which gave the ants simultaneous access to the brightly illuminated and dimly illuminated arena chambers. The cartridge also functioned as an aspirator for collecting the ants in the field (Fig. 2). As a result, the initial collection of the test ants was the only manipulation they received. When used as an aspirator, a tightly fitting plastic ring was slipped over the 4 exit slits. A piece of rubber tubing was attached to the upper end of a central vent in the lid of the cartridge, and an "L"-shaped tube was inserted into a hole near the edge of the lid.

For each test, 40–60 adult worker ants were collected from a raiding column near the bivouac. The cartridge was transported to the laboratory in a dark container. In the laboratory, the cartridge was lowered into the arena. Initially, the cartridge was supported above the floor of the arena by 4 cubes of plastic that projected centrally from the base of each vertical arena partition, far enough to support the outer slip ring. To start the test the cartridge was pushed down, which caused it to slide down through the slip ring, thus simultaneously opening the 4 exit slits.

To test the ants' responses to the presence of each other, another series of

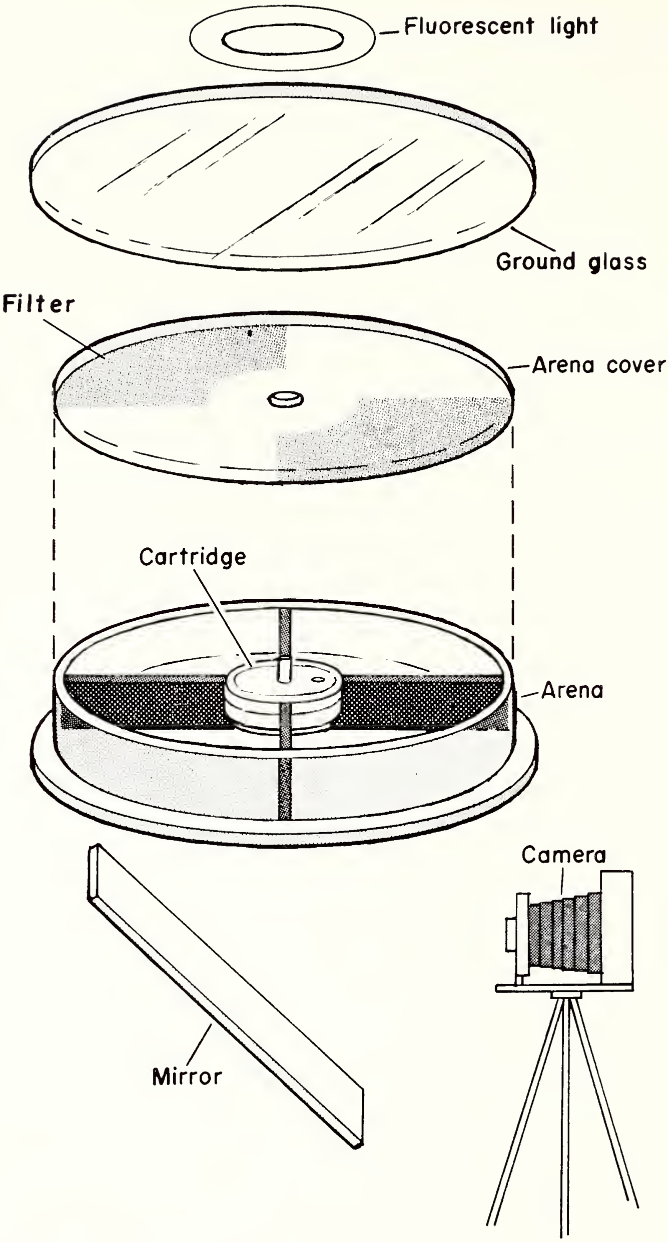

Fig. 1. Apparatus used to test responses of ants to illumination. The cartridge is shown in place in the arena. To test the responses of ants to the presence of each other, the fluorescent light was replaced with an infrared light source.

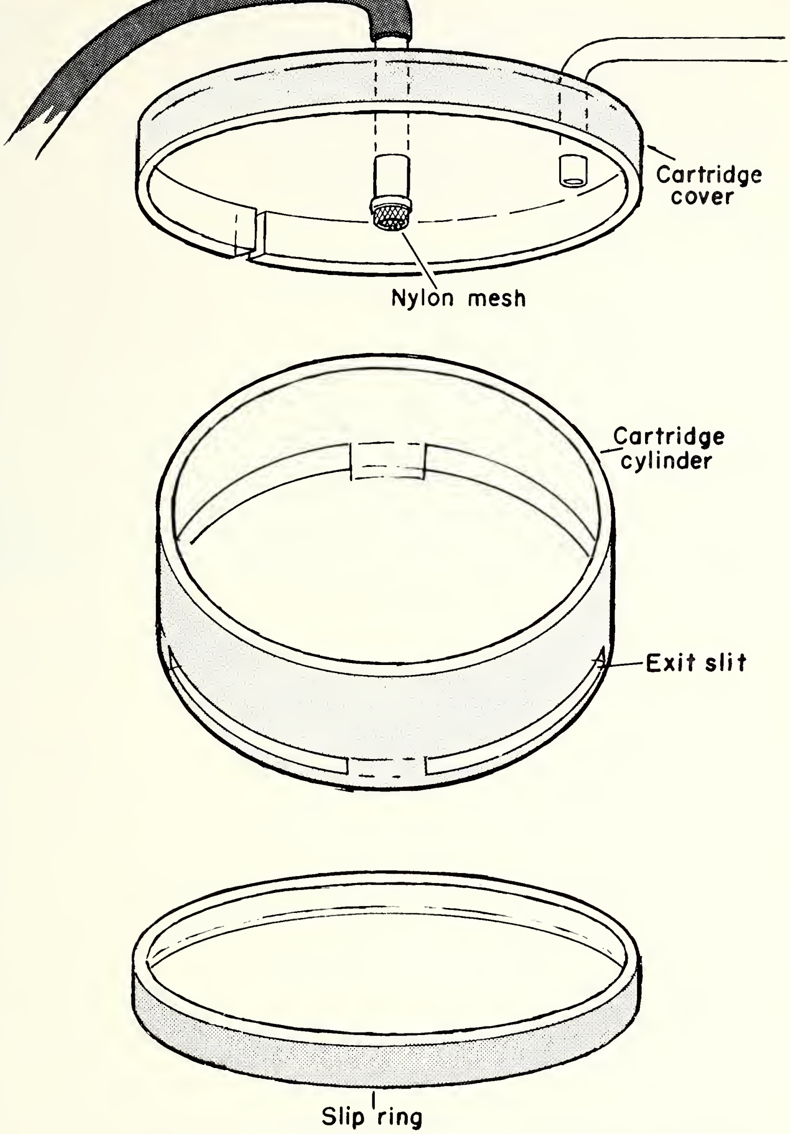

Fig. 2. Central cartridge used for behavioral tests. When used in the field as an aspirator, the plastic ring is slipped over the cartridge to seal the four exit slits. The rubber tubing and "L"-shaped plastic tube in the lid of the cartridge are removable.

experiments was conducted in an identical arena, but no visible light was used. Instead, illumination for photography was provided by 4 150-watt flood lamps that were sealed behind gelatin filters that passed only wavelengths greater than 720 mμ.

TABLE 1. Percentage of ants in central cartridge and arena quadrants after 1 minute.

Colony #	Phase day[1]	Bright-dim test % ants in bright	Bright-dim test % ants in dim	Bright-dim test % ants in cartridge	Infrared test % ants in cartridge
66N-2	N-3	33	47	20	47
	N-7	33	48	19	—
	N-10	26	33	41	28
	N-17	11	49	40	48
	S-2	—	—	—	58
	S-8	0	17	83	49
	S-9	2	65	33	44
	S-10	0	48	52	51
	S-14	—	—	—	58
	S-15	—	—	—	48
	S-16	0	0	100	100
	S-18	0	0	100	—
66N-7	N-4	26	63	11	31
	N-11	29	42	29	16
	S-2	0	0	100	—
	S-3	—	—	—	53
	S-5	0	0	100	53
	S-7	0	0	100	100
	S-14	0	0	100	—
	S-17	0	0	100	100
66N-13	N-10	53	38	9	30
	N-16	57	21	22	15
	S-1	0	0	100	100
	S-7	0	13	87	95
	S-10	0	0	100	77
	S-13	0	0	100	100
72N-3	N-3	34	33	33	28
	N-7	24	50	26	10
	N-13	23	44	33	42
	N-14	79	10	11	18
	S-6	1	10	89	75
	S-7	0	0	100	100
	S-17	0	0	100	100
	S-20	0	22	78	100

[1] N–nomadic; S–statary

Each series of tests lasted for 2 min. To record the position of the ants throughout each test, a photograph was taken at 5 sec intervals from beneath the apparatus. In the "bright-dim" tests, the fluorescent light remained on throughout the test. In the "infrared" series, the infrared light source was electrically programmed to be on for 1.5 sec during each 5 sec interval. Because the infrared light was not visible to the experimenter, a buzzer that was synchronized with the light provided the signal to take a photograph.

RESULTS

Results of tests conducted with 4 colonies of *N. nigrescens* are presented in Table 1, which shows the percentage of ants in the central cartridge and arena quadrants of the "bright-dim" and "infrared" tests after 1 min of each 2 min

Fig. 3. Characteristic pattern of movement in "bright-dim" tests during nomadic phase. The ants are in the central cartridge and all 4 arena quadrants. They are well spaced and moving rapidly.

test. For reasons that will be discussed below, the best measure of the ants' response to illumination is the percentage located in the 2 brightly illuminated arena quadrants. The median percentage of ants taken from nomadic colonies is 31%, as compared to 0% for statary ants.

If we consider the percentage of ants in the dimly illuminated arena quadrants, we find that the median for nomadic ants is 44%, whereas the value for statary ants is again 0%. At first, this may seem to contradict the results obtained from analyzing the percentage of ants in the brightly illuminated quadrants. The discrepancy is resolved by considering the percentage of ants remaining in the central cartridge. During the nomadic phase, the median percentage of ants in the cartridge is 25%. During the statary phase, by contrast, the median is 100%. Thus, the data indicate that nomadic ants tend to leave the central cartridge and enter into either the brightly or dimly illuminated quadrants of the arena. Statary ants tend to remain in the central cartridge throughout the test. If they leave the cartridge they invariably enter into the dimly illuminated quadrants.

The large difference in the number of ants remaining in the central cartridge during the nomadic and statary phases also existed when the tests were conducted under conditions in which the central cartridge and all 4 arena quadrants were

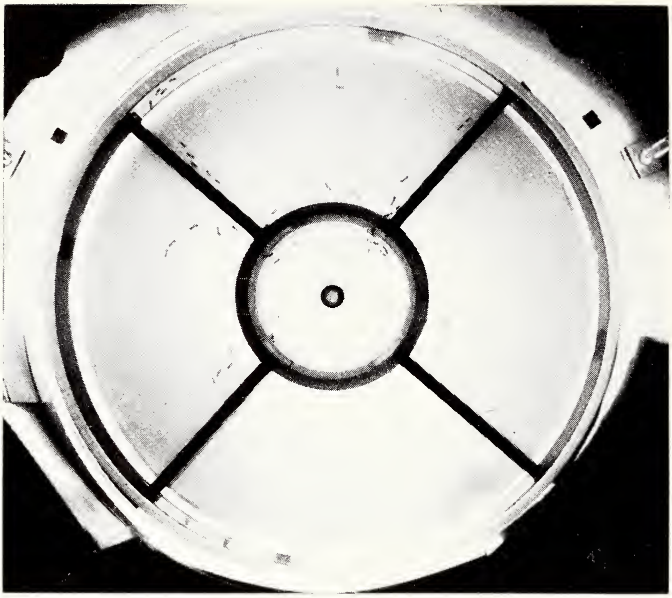

FIG. 4. Characteristic pattern of movement in "infrared" tests during the nomadic phase. As in the "bright-dim" series, the ants occupy all areas of the apparatus.

uniformly illuminated with infrared light. In this series of tests, the median percentage of ants remaining in the cartridge after 1 min was 28% for nomadic ants, as compared to 77% for statary ants.

In addition to the quantitative data presented in Table 1, the photographs used to record the location of the ants throughout each test also revealed striking qualitative differences in the behavior of the ants during the 2 phases. Before the start of a nomadic test, the ants were typically positioned uniformly around the edge of the central cartridge. When the test began, the ants left the cartridge and established columns in the arena quadrants. Regardless of which quadrants they were in, the ants ran rapidly, were well spaced, and exhibited no tendency to cluster. This pattern of behavior was exhibited by the ants during both the "bright-dim" and "infrared" tests (Figs. 3, 4).

The behavior of ants taken from statary colonies was quite different (Figs. 5, 6). Before the start of a test, the ants were usually clustered together in one small section of the cartridge. The clusters varied in degree, but the ants rarely occupied the entire cartridge. In 12 out of 18 "bright-dim" tests conducted with statary ants, the individuals formed into tight clusters that remained in the cartridge throughout the entire test. In 8 out of 19 statary "infrared" tests, similar clusters were formed. It is significant that no such clusters were ever observed during tests conducted with ants taken from nomadic colonies.

FIG. 5. Characteristic pattern of movement in "bright-dim" tests during statary phase. The ants are clustered tightly at the edge of the cartridge.

DISCUSSION

The results of these behavioral tests indicate that workers of *N. nigrescens* respond differently to illumination during the nomadic and statary phases. In southeastern Arizona, *N. nigrescens* has adapted to conditions of high temperatures and low humidity by conducting most of its raiding and emigration activities at night. This correlates with my findings that the ants are always photonegative, although the degree of their photonegativity shifts during the 2 phases of each behavioral cycle.

During the statary phase, the ants often exhibit a marked tendency to cluster tightly together in the central cartridge of the experimental apparatus, regardless of the intensity of illumination. Although the specific cause of the clustering behavior is not known, a reasonable hypothesis is that it is due to the ants' responsiveness to chemical and tactile stimuli arising from other workers. The results of this experiment indicate that the response of the ants to the presence of each other is so strong during the statary phase that it can often override their negative reaction to illumination.

It is well known that the responses of many species of insects to stimuli of constant physical intensity are influenced by environmental factors such as temperature and humidity, and by internal factors, including age, sex, and physiological condition. For example, studies of waterscorpions (Holmes, 1905),

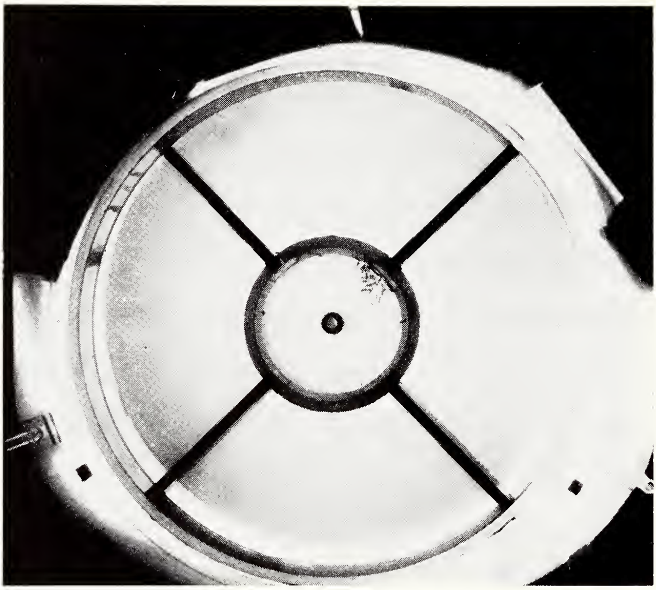

Fig. 6. Characteristic pattern of movement in "infrared" tests during the statary phase. As in the "bright-dim" series, the ants are clustered in the cartridge and remain there throughout the test.

mayflies (Allee and Stein, 1918), drone flies (Dolley and White, 1951), and mosquitoes (Chiba, 1967) indicate that decreasing temperatures result in a shift towards photonegativity. The general consensus of these investigators is that any environmental factor that lowers the organism's excitability tends to increase its negative photoreactivity.

Changes in patterns of orientation with respect to light can also be caused by corresponding changes in stimuli that originate within the organism. Newly hatched larvae of the hawk moth are strongly photopositive, but just prior to pupation the mature larvae become increasingly photonegative (Beetsma *et al.*, 1962). These investigators also showed that injection of the hormone ecdysone could induce the photonegative response. Similar changes in response to illumination as a function of physiological condition have been found in tabanid flies (Shamsuddin, 1966) and milkweed bugs (Barrett and Chiang, 1967).

Orientation towards chemical stimuli can also be influenced by external environmental and internal physiological factors. An investigation that is particularly relevant to the present study was conducted by Goldsmid (1967) on the blue tick, *Boophilus decoloratus*. Newly hatched tick larvae exhibit a strong negative reaction towards light. At this developmental stage, however, the larvae also aggregate together in clusters by orienting towards chemicals secreted by other larvae. This clustering tendency overrides the individuals' negative response towards light. If the cluster is mechanically broken and the larvae scattered within their container, they invariably reaggregate in approximately the same location. After one week, changes in physiological conditions associated with maturation eliminate the tendency to aggregate, and at this time the larvae also become markedly photopositive.

The results of the present study show that workers of the army ant *N. nigrescens* respond differently to illumination and to the presence of conspecifics during the nomadic and statary phases. Based on the studies cited above, it is reasonable to hypothesize that the changes in the ants' responsiveness may be caused by corresponding changes in their degree of excitation during the 2 phases. The nomadic phase is initiated by intense stimulation imparted to the adult worker population by the eclosing callows, and is maintained by equivalent stimulation derived from the developing larval brood (Schneirla, 1957). It is possible that the resulting increase in adult worker excitation and activity causes them to be less photonegative and less responsive to chemicals secreted by other workers. When the larval brood completes its development and pupates, there is a sharp decline in the intensity of social stimulation in the nest. The overall level of excitation is lower, and this causes the workers to exhibit an increase in their photonegativity and in their sensitivity to conspecifics. In the case of the army ants, as in the blue tick, the ants' increased sensitivity to other ants seems to override their increased photonegativity.

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